

THE ENDEMIC VOLE *MICROTUS* (*TYRRHENICOLA*) (ARVICOLIDAE, RODENTIA) FROM MONTE TUTTAVISTA (SARDINIA, ITALY): NEW PERSPECTIVES FOR PHYLOGENY AND BIOCHRONOLOGY

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Resum

Microtus (*Tyrrhenicola*) *henseli* és un talpó fòssil endèmic que va viure a Còrsega i Sardenya des del Pleistocè Mitjà a l'Holocè. S'han reconegut diferents poblacions de *Tyrrhenicola* a través de diferents graus evolutius que presenten una posició sistemàtica encara controvertida. S'han duit a terme algunes anàlisis de diverses poblacions de *Tyrrhenicola* provinents de les fissures recentment estudiades de Monte Tuttavista. Les poblacions estudiades mostren diferents distribucions de morfotipus que permeten reconèixer diferències als graus evolutius que faciliten la ubicació de les diferents poblacions a la seqüència fòssilífera.

Paraules clau: Sardenya, Pleistocè, micromamífers, *Tyrrhenicola*, morfometria

Abstract

Microtus (*Tyrrhenicola*) *henseli* is an endemic fossil vole widespread in Sardinia and Corsica during Middle Pleistocene and Holocene. Though different evolutionary degrees have been recognised between different populations of *Tyrrhenicola* its systematic position is still controversial. Some analyses on several populations of *Tyrrhenicola* from the recently studied fissure fillings of Monte Tuttavista have been carried out, the studied populations show different morphotype distributions that allowed recognising differences in evolutionary degrees helping the sequencing of the different populations.

Keywords: Sardinia, Pleistocene, small mammals, *Tyrrhenicola*, morphometry.

INTRODUCTION

The genus *Tyrrhenicola* has been instituted by Forsyth Major in 1905 to describe the insular fossil vole remains coming from Corsica and Sardinia discovered by Cuvier in 1823 and is now considered a subgenus of *Microtus*. Though considering it at a subgeneric level, for a purpose of simplicity from now on it will be called just *Tyrrhenicola*. *Tyrrhenicola* (Arvicolidae, Rodentia, Mammalia) is an endemic fossil vole widespread in Sardinia and Corsica during Middle Pleistocene and Holocene, including a single described species *Tyrrhenicola henseli*. Though different evolutionary degrees have been recognised between different populations of *T. henseli* (Mezzabotta *et al.*, 1995), the systematic position and the phylogenetic relationships of *Tyrrhenicola* are still controversial.

After the institution of the new genus *Tyrrhenicola* by Forsyth Major, Chaline (1972), following the considerations of Hinton (1926), not only suggested that it represented an insular differentiation of *Terricola*, because of its skull features and the presence of a pitemyan rhombus in the first lower molars, but also that they belong to the same

subgenus *Microtus* (*Terricola*) and proposes an evolution from some *Allophaiomys* forms like the other *Terricola*.

On the contrary, van der Meulen (1973) believes the similarities with *Terricola* to be only a parallelism and propose an evolution from *Allophaiomys pliocaenicus*, suggesting immigration to Sardinia during Early Pleistocene.

Later on, Brunet-Lecomte & Chaline (1990) further suggest that *Tyrrhenicola henseli* may represent an archaic branch of the Mediterranean group of *Terricola* they suppose to be derived from an evolved form of *Allophaiomys*, *A. chalinei*, which might have reached Sardinia and Corsica during the early Middle Pleistocene.

Mezzabotta *et al.* (1995), on the basis of some morphometric analyses, propose an evolution from the *Allophaiomys ruffoi-burgondiae* group and an immigration event dated late Early or early Middle Pleistocene throughout the Tuscan archipelago.

With the exception of the paper of Brandy (1978), all the *Tyrrhenicola* populations recovered until a few years ago in Sardinia or Corsica seem to be already evolved, none of them presenting archaic features that could help us in correlating with continental species. Indeed Brandy

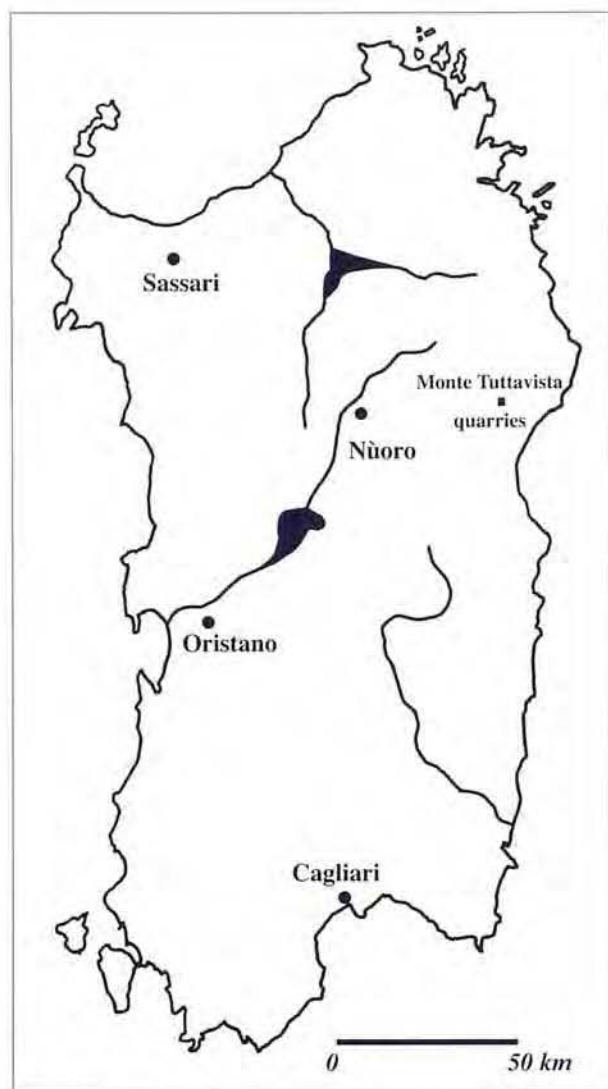


Fig. 1. Localization of Monte Tuttavista quarries.

Fig. 1. Localització de les pedreres de Monte Tuttavista.

(1978), studying the remains from Capo Figari (Sardinia), recognised the presence of a *Tyrrhenicola* more archaic than those recovered before. Later on Cordy (1997) and Sondaar (2000) quote a small sized species from quarry Xg3 of Monte Tuttavista (Sardinia). All these authors suggest it to be a different species from *Tyrrhenicola henseli* and emphasize its smaller size. Indeed size increase in insular small mammal faunas is a well known evolutionary pattern, that affects different families of small mammals in different islands. The Pleistocene Sicilian giant dormouse *Leithia melitensis* (ADAMS, 1863) and the Late Miocene (and Early Pliocene?) murids of the genus *Microtia* and cricetids of the genus *Hattomys* in the palaeoisland(s) of Gargano (Southern Italy) are perfect examples (Freudenthal, 1976, 1985; Abbazzi *et al.*, 1993; Petruso, 2002). The Cretan Pleistocene murids of the endemic genus *Kritimys*, with the temporal succession of three species, *Kritimys* aff. *K. kiridus* – *Kritimys kiridus* (BATE, 1942) – *Kritimys catreus* (BATE, 1912), are another good example of an evolutionary lineage whose members increase in size (Mayhew, 1977). Still in Sardinia the

evolution from the small sized form *Rhagapodemus azzarolii* ANGELONE & KOTSAKIS, 2001 (Mandriola, early Middle Pliocene) through *Rhagapodemus minor* (BRANDY, 1978) (found also in Capo Figari and quarry Xg3) to the bigger *Rhagamys orthodon* (HENSEL, 1856) (widespread in Sardinia during late Middle Pleistocene and Late Pleistocene) is very representative (Angelone & Kotsakis, 2001).

New analyses on several populations of *Tyrrhenicola* from the recently studied fissure fillings of Monte Tuttavista (Abbazzi *et al.*, 2004; Rook *et al.*, 2004) have been carried out. The studied populations show different morphotype distributions that allowed to recognise differences in evolutionary degrees, helping the sequencing of the different populations and showing a general trend towards an increase in the complexity of the anteroconid, with a progressive development of T7 and sometimes the presence of incipient T6 and T9.

MATERIALS AND METHODS

Monte Tuttavista (Orosei, Nuoro) is located in the north-eastern side of Sardinia (Fig. 1) and on its flanks numerous limestone quarries are active. Thanks to the collaboration between the Soprintendenza per i Beni Archeologici delle Province di Sassari e Nuoro and the quarries owners, it has been possible to recover the bony breccias filling of these calcareous fissures (Cordy, 1997). Both large and small mammals, as well as amphibians, reptiles and birds have been recovered and more than 80.000 specimens have been collected. After a preliminary analysis, about 70 taxa have been identified. They can be ascribed to four different faunal complexes, ranging in time from the Late Pliocene to the Late Pleistocene (Palombo *et al.*, 2003; Abbazzi *et al.*, 2004). In the present paper results will be presented about the *Tyrrhenicola* remains coming from 5 of these fissure fillings that take their names from the quarries where they have been recovered: quarry VI banco6, quarry X g3, quarry XI g3, quarry XI "canide" and quarry XI "dic. 2001".

Hundreds of *Tyrrhenicola* specimens were present in each quarry, but a sample of about 30 to 40 first lower molars *per* quarry have been chosen. They have been described and attributed to the main morphotypes recognized by Mezzabotta *et al.* (1995) and frequency percentages have been calculated for each quarry. Moreover twenty-three different measurements on the occlusal surface of M1s have been taken following Brunet-Lecomte (1990) method (Fig.2), as well as 7 indices:

$$AL = (V6 - V3) / V6 * 100$$

$$LW = V6 / V21$$

$$LW2 = V6 / V27$$

$$LW3 = V6 / V2$$

$$RP = (V4 - V3) / V6 * 100$$

$$IAT2T3 = V26 / V27 * 100$$

$$IAT4T5 = V24 / V21 * 100$$

Principal Component Analyses and ANOVAs have been performed. Analyses have been carried out using SPSS 11.0 for Windows installed on a PC of the University of Roma Tre.

RESULTS

After a description and a qualitative analysis, several differences showed up between the different populations from Monte Tuttavista quarries (Fig. 3). As to quarry VI banco6 the majority of the specimens showed a narrow neck between LRA4 and BRA3, a T7 well developed and T6 almost always present even if with different developmental stages. T4 and T5 opposite and confluent and always verging towards the posterior part of the tooth. On the contrary, specimens from quarry X g3 had a very slightly developed anteroconid. T6 and T7 only outlined, while T9 was always lacking. The neck between LRA4 and BRA3 was always large and T4/T5 not confluent.

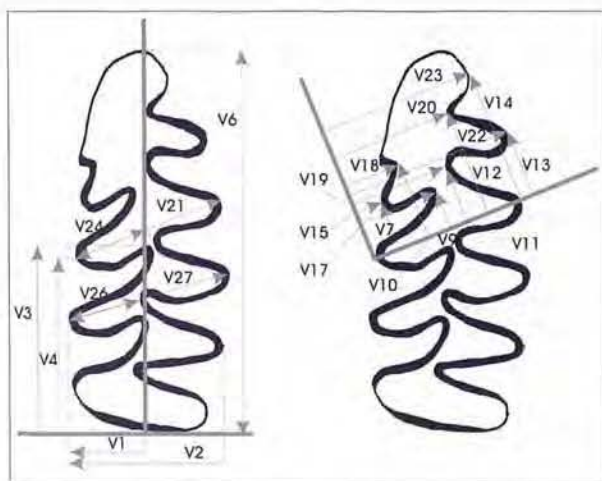


Fig. 2. Main measurements taken on the occlusal surface of *Microtus* (*Tyrrenicola*) M1, modified from Brunet-Lecomte (1990): V1: width of the lingual part of the tooth; V2: total width across the axis; V3: length along the axis of the posterior part on BRA2; V4: length along the axis of the posterior part on BSA2; V6: total length along the axis; V7: length of BSA3 across the T4/T5 axis; V9: length of BRA3 across the T4/T5 axis; V10: length of BSA4 across the T4/T5 axis; V11: length of LRA4 across the T4/T5 axis; V12: length of LRA5 across the T4/T5 axis; V13: length of LSA4 across the T4/T5 axis; V14: length of LSA5 across the T4/T5 axis; V15: distance of BSA3 from T4 along T4/T5 axis; V17: distance of BRA3 from T4 along T4/T5 axis; V18: distance of BRA4 from T4 along T4/T5 axis; V19: distance of LRA4 from T4 along T4/T5 axis; V20: distance of LRA5 from T4 along T4/T5 axis; V21: width along T4/T5; V22: distance of LSA4 from T4 along T4/T5 axis; V23: distance of LSA5 from T4 along T4/T5 axis; V24: width of the buccal part of T4/T5; V26: width of the buccal part of T2/T3; V27: width along T2/T3. Terminology follows van der Meulen (1973).

Fig. 2. Mesures principales prises à la surface occlusale de l'M1 de *Microtus* (*Tyrrenicola*), selon Brunet-Lecomte (1990), modifié. V1: amplitude de la part linguale de la dent; V2: amplitude totale à travers de l'axe; V3: longueur au long de l'axe de la part postérieure de BRA2; V4: longueur au long de l'axe de la part postérieure de BSA2; V6: longueur totale au long de l'axe; V7: longueur de BSA3 à travers de l'axe T4/T5; V9: longueur de BRA3 à travers de l'axe T4/T5; V10: longueur de BSA4 à travers de l'axe T4/T5; V11: longueur de LRA4 à travers de l'axe T4/T5; V12: longueur de LRA5 à travers de l'axe T4/T5; V13: longueur de LSA4 à travers de l'axe T4/T5; V14: longueur de LSA5 à travers de l'axe T4/T5; V15: distance de BSA3 des de T4 au long de l'axe T4/T5; V17: distance de BRA3 des de T4 au long de l'axe T4/T5; V18: distance de BRA4 des de T4 au long de l'axe T4/T5; V19: distance de LRA4 des de T4 au long de l'axe T4/T5; V20: distance de LRA5 des de T4 au long de l'axe T4/T5; V21: amplitude au long de T4/T5; V22: distance de LSA4 des de T4 au long de l'axe T4/T5; V23: distance de LSA5 des de T4 au long de l'axe T4/T5; V24: amplitude de la part buccale de T4/T5; V26: amplitude de la part buccale de T2/T3; V27: amplitude au long de T2/T3. La terminologie suit van der Meulen (1973).

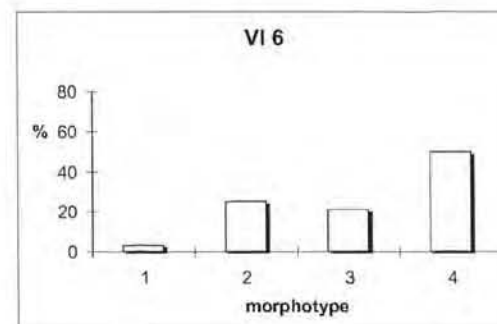
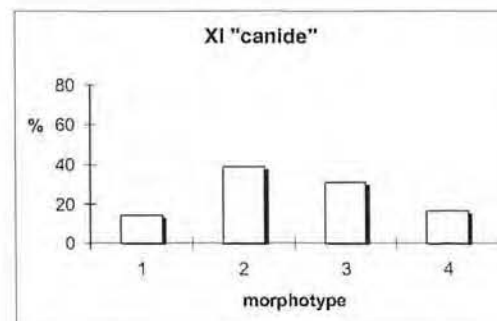
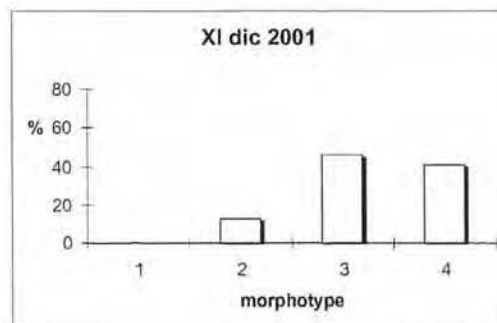
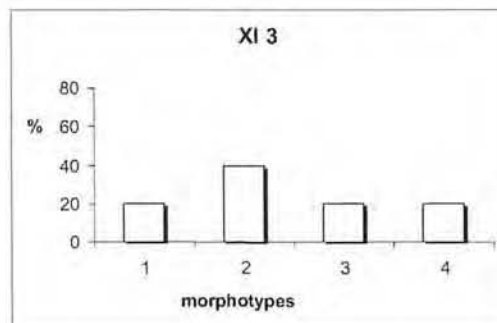
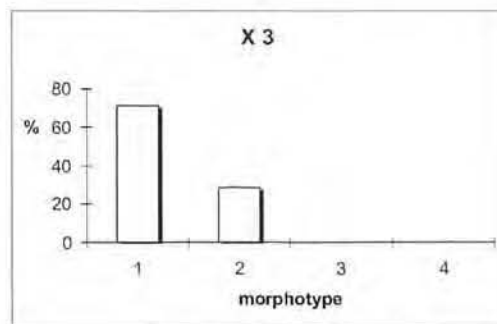


Fig. 3. Histograms of the morphotypes frequencies of the Monte Tuttavista populations (expressed as a percentage).

Fig. 3. Histogrammes de les fréquences de morfotipus de les poblacions de Monte Tuttavista (expressats com a percentatges).

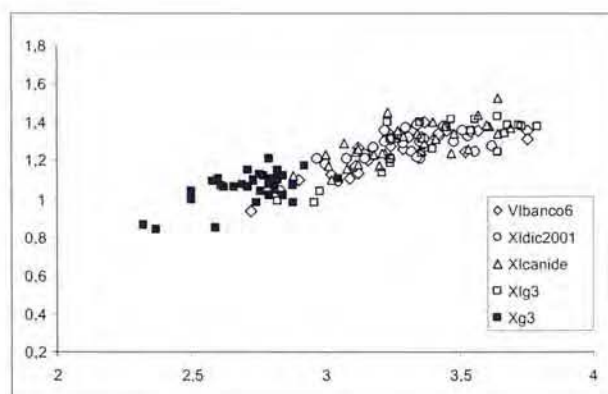


Fig. 4. Length against width plot for all the populations.

Fig. 4. Relació entre la llargària i l'amplària per a totes les poblacions.

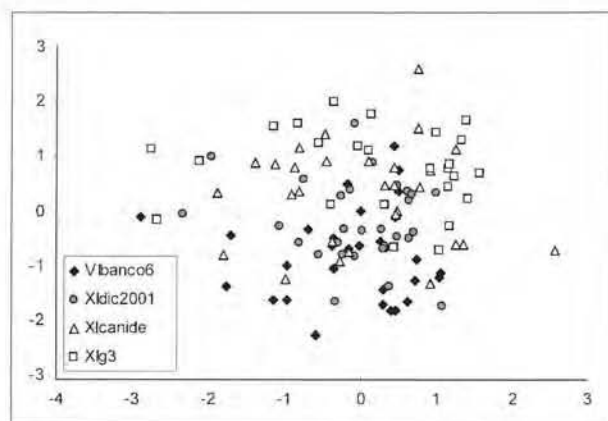


Fig. 5. Principal Component Analysis on V1, V2, V3, V4, V6, V21, V24, and V27 for quarry XI g3, XI "canide", XI "dic.2001" and VI banco6.

Fig. 5. Anàlisi de Components Principals de V1, V2, V3, V4, V6, V21, V24, i V27 per a les pedreres XI g3, XI "canide", XI "dic.2001" i VI banco6.

The other quarries populations showed intermediate features such as a short and rounded anteroconid in quarry XI g3 specimens, or T6 and T7 retrovergent but with a narrow neck in quarry XI "dic. 2001", or with a very variable neck – from very narrow to very wide – in quarry XI "canide" specimens.

Once described, the teeth have been attributed to the four main morphotypes of Mezzabotta *et al.* (1995), and percentage frequencies have been calculated. The calculation of frequencies showed interesting patterns (Table 1): quarry X g3 specimens belong only to morphotypes 1 and 2, with a clear prevalence of number 1 (71.4%). First lower molars of XI g3 have been attributed to all the four morphotypes, with a prevalence for number 2 (40%). Quarry XI "canide" has an almost equal percentage of morphotypes 2 and 3 (38.8% and 30.6% respectively), while the populations from VI banco6 and XI "dic. 2001" seem to be the more evolved, with a prevalence of morphotypes 3 and 4. It has been therefore possible to establish a sort of relative sequence between Monte Tuttavista fissures (Fig. 4) on the basis of the prevalent morphotype within the populations, where quarry X g3 is the more archaic and VI banco6 and XI "dic. 2001" the more evolved.

| Quarries | Morphotype frequencies (%) | | | |
|----------------|----------------------------|------|------|------|
| | 1 | 2 | 3 | 4 |
| X g3 | 71.4 | 28.6 | | |
| XI g3 | 20 | 40 | 20 | 20 |
| XI "canide" | 14.3 | 38.8 | 30.6 | 16.3 |
| XI "dic. 2001" | | 12.8 | 46.2 | 41.0 |
| VI banco6 | 3.6 | 25.0 | 21.4 | 50.0 |

Table 1. Morphotype frequency percentages of the five quarries.

Taula 1. Percentatges de freqüència dels morfotipus a les cinc pedreres.

| Component | Total | % of Variance | Cumulative % |
|-----------|-------|---------------|--------------|
| 1 | 6.086 | 76.072 | 76.072 |
| 2 | 0.934 | 11.672 | 87.745 |
| 3 | 0.266 | 3.319 | 91.063 |
| 4 | 0.230 | 2.876 | 93.940 |
| 5 | 0.202 | 2.520 | 96.459 |
| 6 | 0.148 | 1.853 | 98.312 |
| 7 | 0.088 | 1.104 | 99.416 |
| 8 | 0.047 | 0.584 | 100 |

Table 2. Eigenvalues of Principal Component Analysis on V1, V2, V3, V4, V6, V21, V24, V26 and V27 for quarry XI g3, XI "canide", XI "dic.2001" and VI banco6.

Taula 2. Eigenvalues de l'Anàlisi de Components Principals sobre V1, V2, V3, V4, V6, V21, V24, V26 i V27 per a la pedrera XI g3, XI "canide", XI "dic.2001" i VI banco6.

| Variables | Component | |
|-----------|-----------|--------|
| | 1 | 2 |
| V1 | 0.905 | -0.052 |
| V2 | 0.961 | 0.023 |
| V3 | 0.745 | 0.584 |
| V4 | 0.530 | 0.821 |
| V6 | 0.801 | 0.283 |
| V21 | 0.964 | -0.026 |
| V24 | 0.914 | -0.115 |
| V27 | 0.929 | 0.112 |

Table 3. Factor Loadings of Principal Component Analysis on V1, V2, V3, V4, V6, V21, V24, V26 and V27 for quarry XI g3, XI "canide", XI "dic.2001" and VI banco6.

Taula 3. Factor Loadings de l'Anàlisi de Components Principals sobre V1, V2, V3, V4, V6, V21, V24, V26 i V27 per a la pedrera XI g3, XI "canide", XI "dic.2001" i VI banco6.

Another simple analysis, such as the relationship between width and length of the M₁, has been performed (Fig. 5), showing a high correlation coefficient ($R^2 = 0.746$) and a differentiation in two main groups: one composed mainly by quarry Xg3 specimens and the other by the other populations.

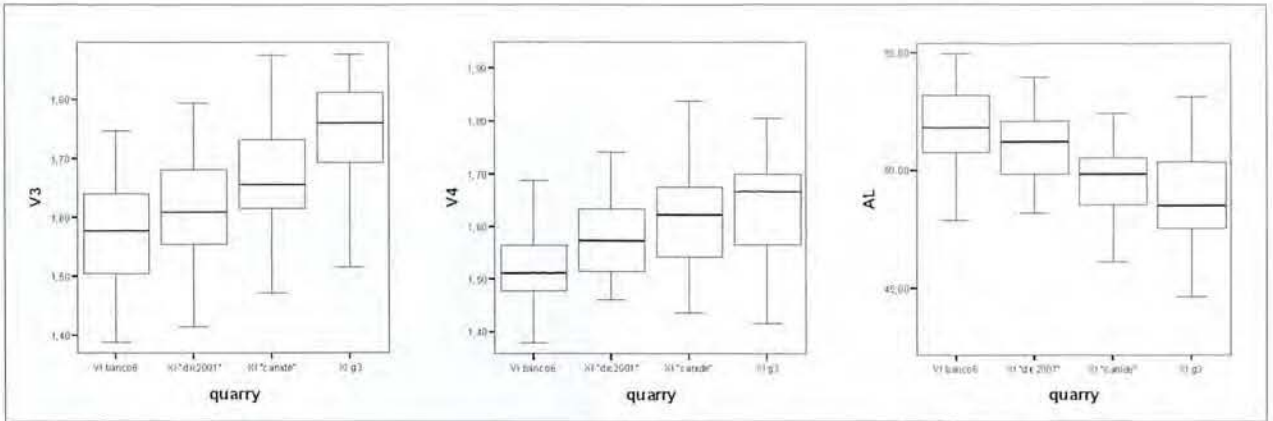


Fig. 6. Boxplots of a: V3; b: V4; c: AL.

Fig. 6. Boxplots de a: V3; b: V4; c: AL.

| Quarry | N | Mean V3 | Std. Dev. V3 | Mean V4 | Std. Dev. V4 | Mean V6 | Std. Dev. V6 | Mean AL | Std. Dev. AL |
|--------------|----|----------|--------------|----------|--------------|---------|--------------|----------|--------------|
| VI banco6 | 30 | 1.58 | 0.09 | 1.52 | 0.08 | 3.28 | 0.23 | 51.90 | 1.75 |
| XI "canide" | 30 | 1.67 | 0.11 | 1.61 | 0.09 | 3.31 | 0.23 | 49.56 | 1.37 |
| XI "dic2001" | 30 | 1.62 | 0.08 | 1.58 | 0.09 | 3.29 | 0.19 | 50.79 | 1.94 |
| XI g3 | 25 | 1.74 | 0.11 | 1.64 | 0.09 | 3.39 | 0.26 | 48.73 | 2.44 |
| ANOVA | | p<0.0001 | | p<0.0001 | | N.S. | | p<0.0001 | |

Table 4. ANOVAs results for V3, V4, V6 and AL.

Taula 4. Resultats de l'ANOVA per V3, V4, V6 i AL.

It is therefore simple to identify quarry Xg3, though none of the above mentioned analyses has been able to discriminate between the other four quarries populations. That is why we decided to apply a simple morphometric method such as that of Brunet-Lecomte (1990) measurements, with the aim to determine if a difference between the populations exists and, in that case, which are the variables responsible for such a differentiation.

Several Principal Component Analyses have been performed. A first one with all the variables together, then using only the measurements of the anteroconid complex, or using both the variables of the main body of the tooth and the horizontal measurements of the anteroconid, or the contrary: the variables of the main body of the tooth and the vertical measurements of the anteroconid. The best resolution we obtained was using only the main variables of the tooth excluding those describing the anteroconid (Table 2). In this case, a good differentiation is visible on a bivariate plot along Axis 2, where two main groups are visible (Fig. 6): one composed by quarry VI banco6 and quarry XI "dic.2001" and the other formed by XI g3 and XI "canide". As results from Table 3 the second principal component weight is given mainly by V3 and V4, representing the length of BSA2 and BRA2, respectively, along the tooth axis.

ANOVAs and post-hoc tests have been therefore performed on these two variables to determine their significance in the differentiation of the populations and on V6, the total length, to have a final clue whether the size shows a significant variation or not.

Both V3 and V4 show a significant ANOVA ($p<0.0001$ in both cases; table 4) while the analysis on V6 is not sig-

| (I) Quarry | (J) Quarry | Mean Difference (I-J) | Std. Error | Sig. |
|--------------|--------------|-----------------------|------------|-------|
| VI banco6 | XI "dic2001" | -0.042 | 0.026 | 0.437 |
| | XI "canide" | -0.090* | 0.026 | 0.008 |
| | XI g3 | -0.159* | 0.027 | 0.000 |
| XI "dic2001" | VI banco6 | 0.042 | 0.026 | 0.437 |
| | XI "canide" | -0.048 | 0.026 | 0.325 |
| | XI g3 | -0.117* | 0.027 | 0.001 |
| XI "canide" | VI banco6 | 0.090* | 0.026 | 0.008 |
| | XI "dic2001" | 0.048 | 0.026 | 0.325 |
| | XI g3 | -0.069 | 0.027 | 0.090 |
| XI g3 | VI banco6 | 0.159* | 0.027 | 0.000 |
| | XI "dic2001" | 0.117* | 0.027 | 0.001 |
| | XI "canide" | 0.069 | 0.027 | 0.090 |

* The mean difference is significant at the .05 level.

Table 5. Scheffé test results for V3.

Taula 5. Resultats del test d'Scheffé per a V3.

nificant, meaning size in itself does not vary significantly within the studied populations.

Scheffé test has been performed (Table 5) showing for V3 a significant difference between means of quarry VI banco6 and XI g3 / XI "canide", as well as a difference between quarry XI "dic.2001" and XI g3. The analysis of the homogeneity of subsets of the means (Table 6) shows

| Quarry | N | Subset | | |
|--------------|----|--------|-------|-------|
| | | 1 | 2 | 3 |
| VI banco6 | 30 | 1.576 | | |
| XI "dic2001" | 30 | 1.618 | 1.618 | |
| XI "canide" | 30 | | 1.666 | 1.666 |
| XI g3 | 25 | | | 1.735 |
| Sig. | | 0.458 | 0.346 | 0.078 |

Table 6. Univariate Homogeneous Subsets for V3.

Taula 6. Subconjunts homogenis univariats per a V3.

| (I) Quarry | (J) Quarry | Mean Difference (I-J) | Std. Error | Sig. |
|--------------|--------------|-----------------------|------------|-------|
| VI banco6 | XI "dic2001" | -0.066* | 0.023 | 0.048 |
| | XI "canide" | -0.094* | 0.023 | 0.001 |
| | XI g3 | -0.125* | 0.024 | 0.000 |
| XI "dic2001" | VI banco6 | 0.066* | 0.023 | 0.048 |
| | XI "canide" | -0.028 | 0.023 | 0.678 |
| | XI g3 | -0.060 | 0.024 | 0.113 |
| XI "canide" | VI banco6 | 0.094* | 0.023 | 0.001 |
| | XI "dic2001" | 0.028 | 0.023 | 0.678 |
| | XI g3 | -0.031 | 0.024 | 0.643 |
| XI g3 | VI banco6 | 0.125* | 0.024 | 0.000 |
| | XI "dic2001" | 0.060 | 0.024 | 0.113 |
| | XI "canide" | 0.031 | 0.024 | 0.643 |

* The mean difference is significant at the .05 level.

Table 7. Scheffé test results for V4.

Taula 7. Resultats del test d'Scheffé per a V4.

| Quarry | N | Subset | |
|--------------|----|--------|-------|
| | | 1 | 2 |
| VI banco6 | 30 | 1.519 | |
| XI "dic2001" | 30 | 1.584 | 1.584 |
| XI "canide" | 30 | | 1.613 |
| XI g3 | 25 | | 1.644 |
| Sig. | | 0.057 | 0.100 |

Table 8. Univariate Homogeneous Subsets for V4.

Taula 8. Subconjunts homogenis univariats per a V4.

three subsets, meaning that the means of VI banco 6 and XI "dic.2001" do not differ significantly, that the means of XI "dic.2001" and XI "canide" do not differ significantly and that the means of XI "canide" and XI g3 do not differ significantly. The same analysis (tables 7 and 8) performed on V4 shows two subsets, one composed by VI banco6 and XI "dic.2001", and the other by XI "canide" and XI g3 with XI "dic.2001" that stays in both subsets.

ANOVAs and post-hocs have been performed also on the indices. None of them result in a significant difference between the populations except for AL, the relative elongation of the anterior part of the tooth, (Table 4 and

9) and RP, but with a lower significance level. AL means of quarry VI banco6 and XI g3 / XI "canide" are significantly different, as well as between quarry XI "dic.2001" and XI g3. This leads to a subset pattern similar to that of V3 (table 10).

DISCUSSION AND CONCLUSIONS

The considerable amount of material recovered from the Monte Tuttavista quarries is leading to an extensive study not only of the *Tyrrenicola* specimens, but also of the whole fauna of large and small mammals, allowing comparisons to be made either by an evolutionary and a biochronological point of view. At the beginning of our studies we possessed very few clues about the age of the fissures nor there was a biochronological framework of Sardinian mammal faunas, helping in the stratigraphic constraining of the faunas. Many of the recovered large mammal taxa were new species or even new genera, and the possibility to have even a relative sequence of the quarries was, at the beginning, unlikely.

Unfortunately the morphological qualitative analysis of the populations, even in presence of a high number of specimens, has not proven to be decisive, due to the highly variable characters of the anteroconid complex. The apparent predominance of some features is, in fact, not confirmed by a quantitative statistic analysis of the measurements of the anteroconid complex. As already stated by Mezzabotta *et al.* (1995) we are in presence of a clear mosaic evolutionary pattern, visible even in a very restricted area such as that of the Monte Tuttavista. This is not completely exact for quarry X g3 population that shows indeed a smaller size and a much simpler anteroconid than the other quarries populations. Such features have been already noticed by Cordy (1997) and Sondaar (2000) which suggested the possibilities of a new species of *Tyrrenicola*, possibly related to those archaic remains of Capo Figari quoted by Brandy (1978). Such a possibility is indeed confirmed by the present study, where all the signs indicate a marked difference between quarry Xg3 and all the other *Tyrrenicola* up to day recovered, both qualitatively and quantitatively. The anteroconid is less developed and complicated, leading to a definitely smaller size, the total absence of morphotypes number 3 or 4, and the predominance of number 1; they all strongly suggest for the *Tyrrenicola* of quarry X g3 to be the ancestor species of *T. henseli*. Further morphometric studies and comparisons of this archaic form with other continental taxa will likely help the identification of the ancestor of *Tyrrenicola* (Marcolini *et al.*, in press).

Still uncertainties remained as to the possibility to identify different evolutionary degrees between the other four populations, supposing that they exist.

Morphotypes frequencies are giving the first clue for a possible sequence to be constructed (Fig. 4). Quarry XI g3 and XI "canide" have almost the same percentage of morphotype 2, but while the latter has also a high percentage of number 3, the first has almost equal weights on the other three. Same stands for quarry VI banco6 and

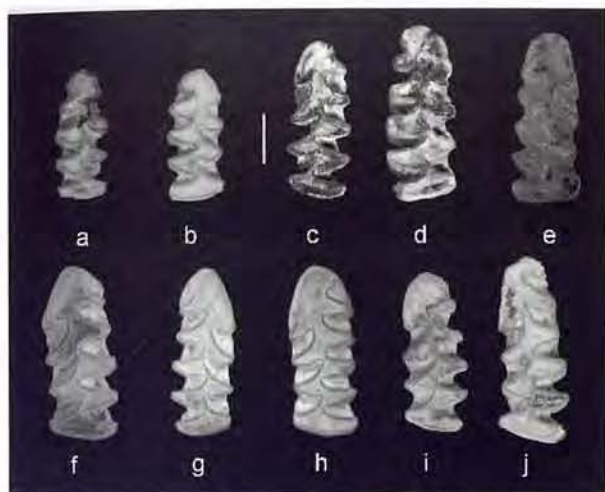


Plate 1. *Microtus (Tyrrenicola)* first lower molars from Monte Tuttavista: a, b: quarry X g3, specimens ORX3ty5 and ORX3ty9; c, d: quarry XI g3, specimens ORXI3ty39 and ORXI3ty 45; e, f: quarry XI "canide", specimens ORXIcty82 and ORXIcty 87; g, h: quarry XI "dic.2001", specimens ORXI2001ty123 and ORXI2001ty129; i, j: quarry VI banco6, specimens ORVI6ty162 and ORVI6ty168. Scale bar represents 1 mm.

Làmina 1. Primers molars inferiors de *Microtus (Tyrrenicola)* de Monte Tuttavista. a, b: pedrera X g3, espècimens ORX3ty5 i ORX3ty9; c, d: pedrera XI g3, espècimens ORXI3ty39 i ORXI3ty 45; e, f: pedrera XI "canide", espècimens ORXIcty82 i ORXIcty 87; g, h: pedrera XI "dic.2001", espècimens ORXI2001ty123 i ORXI2001ty129; i, j: pedrera VI banco6, espècimens ORVI6ty162 i ORVI6ty168. L'escala representa 1 mm.

XI "dic. 2001", where number 4 and 3 are the more represented respectively, while the other frequencies are more variable.

On this basis a possible sequence of the quarries, from the oldest to the youngest, can be XI g3, XI "canide", XI "dic. 2001" and VI banco6. Such an interpretation is in good agreement with the pieces of information coming from the other small mammals and from large mammals (Abbazzi *et al.*, 2004). In order to ameliorate the global knowledge on the stratigraphy of all the quarries, we compared the morphotype percentage frequencies with those of other Sardinian and Corsican sites we were able to find in literature. Unfortunately no radiometric dates exist for any of the Sardinian faunas, while a few are available for Corsica. Published data on *Tyrrenicola* for Capo Figari, Dragonara, Siniscola, Monte San Giovanni, Bonaria (Mezzabotta *et al.*, 1995), Punta di Calcina and Castiglione 3CG (Pereira *et al.*, 2001) have been compared with the percentages we calculated for Monte Tuttavista quarries (Table 11). We were thus able to obtain a relative sequencing of the Sardo-Corsican faunas where *Tyrrenicola* is present and abundant, awaiting for the possibility to obtain radiometric dates of some of the Sardinian sites.

Still the problem risks to remain unsolved for all those sites where only a few first lower molars of *Tyrrenicola* are present. Moreover when we deal with single specimens or a very reduced population, where reliable frequency percentages cannot be computed, to determine with good certainty which is the evolutionary stage of the species – and therefore of the containing

| (I) Quarry | (J) Quarry | Mean Difference (I-J) | Std. Error | Sig. |
|--------------|--------------|-----------------------|------------|-------|
| VI banco6 | XI "dic2001" | 1.111 | 0.487 | 0.163 |
| | XI "canide" | 2.337* | 0.487 | 0.000 |
| | XI g3 | 3.165* | 0.510 | 0.000 |
| XI "dic2001" | VI banco6 | -1.111 | 0.487 | 0.163 |
| | XI "canide" | 1.226 | 0.487 | 0.102 |
| | XI g3 | 2.053* | 0.510 | 0.002 |
| XI "canide" | VI banco6 | -2.337 | 0.487 | 0.000 |
| | XI "dic2001" | -1.226 | 0.487 | 0.102 |
| | XI g3 | 0.828 | 0.510 | 0.456 |
| XI g3 | VI banco6 | -3.165* | 0.510 | 0.000 |
| | XI "dic2001" | -2.053* | 0.510 | 0.002 |
| | XI "canide" | -0.828 | 0.510 | 0.456 |

* The mean difference is significant at the 0.05 level.

Table 9. Scheffé test results for AL.

Taula 9. Resultats del test d'Scheffé per a AL.

| Quarry | N | Subset | |
|--------------|----|--------|--------|
| | | 1 | 2 |
| XI g3 | 25 | -2.635 | |
| VI banco6 | 30 | -1.716 | -1.716 |
| XI "canide" | 30 | -1.571 | -1.571 |
| XI "dic2001" | 30 | | -1.004 |
| Sig. | | 0.234 | 0.587 |

Table 10. Univariate Homogeneous Subsets for AL.

Taula 10. Subconjunts homogenis univariats per a AL.

| | morphotype frequencies (%) | | | |
|---------------------|----------------------------|------|------|------|
| | 1 | 2 | 3 | 4 |
| X g3 | 71.4 | 28.6 | | |
| Capo Figari* | 11.1 | 33.3 | 44.4 | 11.1 |
| Dragonara* | 21.1 | 42.1 | 26.3 | 10.5 |
| XI g3 | 20 | 40 | 20 | 20 |
| Punta di Calcina° | 18.8 | 46.9 | 28.2 | 6.3 |
| XI "canide" | 14.3 | 38.8 | 30.6 | 16.3 |
| Siniscola C* | 11.1 | 44.4 | 22.2 | 22.1 |
| Monte San Giovanni* | 6.9 | 24.1 | 58.6 | 10.3 |
| Siniscola E* | | 16.7 | 66.7 | 16.7 |
| Bonaria* | | 47.4 | 39.5 | 13.1 |
| XI "dic. 2001" | | 12.8 | 46.2 | 41.0 |
| VI banco6 | 3.6 | 25.0 | 21.4 | 50.0 |
| Castiglione 3CG° | | 2.7 | 56.2 | 41.1 |

Table 11. Tentative relative sequence of Corsican and Sardinian *Microtus (Tyrrenicola)* faunas; * data from: Mezzabotta *et al.* (1995); ° data from: Pereira *et al.* (2001).

Taula 11. Seqüència relativa tentativa de les faunes de *Microtus (Tyrrenicola)* corses i sardes; * dades de: Mezzabotta *et al.* (1995); ° dades de: Pereira *et al.* (2001).

fauna – is quite impossible, which is the reason why PCAs have been performed. When we determined all the measurements, especially those taken on the anteroconid, and we performed the PCAs we were hoping to obtain a good resolution in the differentiation of the morphological fields of the species *T. henseli*. What happened instead is that we were able to glimpse a small differentiation only excluding the measurements of the anteroconid features and used only the main tooth variables. This is certainly due to the mosaic evolutionary pattern of which *Tyrrhenicola* is a perfect example. Such a small differentiation, given mainly by V3 and V4, perfectly fits the pattern obtained with the morphotype analysis, with the two main groups composed by quarries VI banco6/XI “dic. 2001” and quarries XI “canide”/XI g3. It is also in good agreement with the patterns summarized by Mezzabotta *et al.* (1995) of an increase in the complexity of the AC and an elongation of the ACC even if we were not able to distinguish a consequent statistically significant increase in the size of the tooth.

Following the Scheffé's test results and its proposed subsets it is possible to hypothesize a more detailed evolutionary sequence of the populations. It starts with quarry XI g3 followed by XI “canide” and XI “dic. 2001” and ending with VI banco6. Within this sequence, size in itself does not vary significantly, as suggested by the PCA and confirmed by the ANOVA, still the complexity and the size of the anteroconid – even if following a mosaic pattern – increase, determining a significant variation in the AL index and a reduction of V3 (Fig. 7). The reduction of V4 attests to the trend toward a backward vergence of triangles T4 and T5 as exemplified in morphotype 4 of Mezzabotta *et al.* (1995, fig. 8).

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